2004

A MULTISTATE CAPTURE-RECAPTURE MODEL USING A POSTERIORI CLASSIFICATION TO ENHANCE ESTIMATION OF MOVEMENT RATES

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The Condor 106:761–767

A MULTISTATE CAPTURE-RECAPTURE MODEL USING *A POSTERIORI* CLASSIFICATION TO ENHANCE ESTIMATION OF MOVEMENT RATES

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Abstract. Biologists commonly use multistate capture-recapture models to estimate movement and survival rates of animals. Recent improvements to genetic and stable-isotope techniques have created the potential for making *a posteriori* determinations of an animal's location. Here, I present a new multistate model structure that incorporates captured animals' backdated locations. To provide data for this model, I developed a computer simulation in which birds moved between two geographic strata during three time periods. Birds were captured and assigned mortality, and multistate capture histories were recorded. I enhanced capture histories for birds using data from simulated stable-isotope analyses. I then used the modified multistate model to estimate survival, movement, and recapture probabilities. I evaluated the ability of stable-isotope data to more precisely estimate movement over a range of recapture and movement rates. In each of nine simulations, information from stable isotopes improved the precision of the movement estimate; estimates and precision of survival and recapture rates did not change. As real stable-isotope data sets become available, this estimation model may be useful to biologists interested in improving precision of movement rates among geographic strata.

Key words: movement rate, multistate models, simulation model, stable isotopes, survival estimate.

Un Modelo Multi-Estado de Captura-Recaptura Usando Clasificación *A Posteriori* para Potenciar la Estimación de Tasas de Movimiento

Resumen. Los biólogos usan generalmente modelos multi-estado de captura-recaptura para estimar las tasas de movimiento y supervivencia de los animales. Las mejoras recientes de las técnicas genéticas y de isótopos estables han creado el potencial de hacer determinaciones *a posteriori* de la localización de un animal. Aquí presento la estructura de un nuevo modelo multi-estado que incorpora las localidades pasadas de animales capturados. Para contar con datos para este modelo, desarrollé una simulación en computadora en la cual las aves se movieron entre dos estratos geográficos durante tres períodos de tiempo. Las aves fueron capturadas y se les asignó un valor de mortalidad, y se registraron las historias de capturas multi-estado. Potencié el uso de las historias de captura de las aves empleando datos simulados de análisis de isótopos estables. Luego usé el modelo multi-estado modificado para estimar las probabilidades de supervivencia, de movimiento y de recaptura. Evalué la habilidad de los datos de isótopos estables para estimar movimiento de modo más preciso en un rango de tasas de recaptura y movimiento. En cada una de las nueve simulaciones, la información de los isótopos estables mejoró la precisión de la estimación de movimiento; las estimaciones y la precisión de las tasas de supervivencia y recaptura no variaron. A medida que estén disponibles datos reales de isótopos estables, este modelo de estimación puede ser útil para los biólogos interesados en mejorar la precisión de las tasas de movimiento entre estratos geográficos.

INTRODUCTION

Biologists commonly use multistate models (Brownie et al. 1993) to estimate movement rates of animals among habitat patches. These models use mark-recapture data, and may also incorporate radio-telemetry data (Powell et al. 2000). Multistate mark-recapture data are limited by biologists' ability to capture animals and assign them to a geographic stratum, which is unknown during periods when the animal is not captured (Brownie et al. 1993). Recently, stable isotopes, molecular genetics, and other forensic clues have been used to determine, *a posteriori*, the location of an animal (Webster et al. 2002). In fact, the potential for these methods is so

Manuscript received 2 December 2003; accepted 11 June 2004.
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TABLE 1. Model expectation structure for simultaneous estimation of survival (S), movement (ψ), and capture (p)probabilities for animals released in stratum 1 in a two-stratum system and recaptured in either stratum 1 or 2 during three capture periods. Note that $0^{(r)}$ in a capture history indicates that an animal was not captured during the period, but that its presence in stratum r was correctly determined by *a posteriori* analyses. ψ_i^{rs} = probability of moving from stratum r to s between sampling occasion i and $i + 1$; S_i^r = probability of animal on stratum r at time i surviving to $i + 1$; p_i^r = probability of animal on stratum r at time i being recaptured at occasion $i + 1$.

Capture history[a]	Probability associated with capture history
0 1 1	$S_2^1 (1 - \psi_2^{12})p_3^1$
0 1 2	$S_2^1 (\psi_2^{12})p_3^2$
1 1 1	$S_1^1 (1 - \psi_1^{12})(p_2^1)\ S_2^1 (1 - \psi_2^{12})p_3^1$
1 2 1	$S_1^1 (\psi_1^{12})(p_2^2)\ S_2^2 (\psi_2^{21})p_3^1$
1 0 1	$[S_1^1 (1 - \psi_1^{12})(1 - p_2^1)\ S_2^1 (1 - \psi_2^{12})p_3^1] + [S_1^1 (\psi_1^{12})(1 - p_2^2)\ S_2^2 (\psi_2^{21})p_3^1]$
1 0 2	$[S_1^1 (1 - \psi_1^{12})1 - (p_2^1)\ S_2^1 (\psi_2^{12})p_3^2] + [S_1^1 (\psi_2^{12})(1 - p_2^2)S_2^2 (1 - \psi_2^{21})p_3^2]$
1 $0^{(1)}$ 1	$S_1^1 (1 - \psi_1^{12})(1 - p_2^1)\ S_2^1 (1 - \psi_2^{12})p_3^1$
1 $0^{(2)}$ 1	$S_1^1 (\psi_1^{12})(1 - p_2^1)\ S_2^2 (\psi_2^{21})p_3^1$
1 $0^{(1)}$ 2	$S_1^1 (1 - \psi_1^{12})(1 - p_2^1)\ S_2^1 (\psi_2^{12})p_3^2$
1 $0^{(2)}$ 2	$S_1^1 (\psi_1^{12})(1 - p_2^2)\ S_2^2 (1 - \psi_2^{21})p_3^2$

[a] 0 = animal was not captured in this period; 1 = animal captured in stratum 1; 2 = recaptured in stratum 2.

great that Smith et al. (2003) encouraged ornithologists to begin collecting feather tissue for use in these analyses as a part of regular banding protocol.

Biologists can use stable-isotope ratios (e.g., $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, δD, and $\delta^{87}Sr$) to determine where birds and other animals have been in a previous time period (Hobson 1999, Webster et al. 2002). Stable isotopes are useful in providing previous locations of animals because tissues in individuals reflect the isotopic signature of their foods, and biogeochemical processes cause these signatures to vary spatially (Hobson 1999). Feathers are especially useful in backdating an animal's location, as feathers have no turnover of tissue until molt occurs (Hobson 1999). For example, the Wood Thrush (*Hylocichla mustelina*) does not molt the rectrices until late summer (Pyle et al. 1987), and the rest of the flight feathers are replaced before migration (Vega-Rivera et al. 1998). During the breeding season, the rectrices provide a record of the bird's location at the end of the previous breeding season. Thus, a capture at time t has the potential to provide location data for the bird at time t and time $t - 1$.

In addition to stable-isotope approaches, biologists could backdate stratum assignments through analysis of area-specific genetic signatures from avian parasites (Webster et al. 2002). I propose that this information may be used to enhance information on movement patterns derived from a multistate model. Present model structures, however, do not allow for the addition of retrospective data. Therefore, my goal was to develop a model structure that would incorporate the additional information regarding animal movements provided by stable-isotope or other data. I determined the benefits of this additional information across a range of recapture rates, movement rates, and sample sizes.

METHODS

MODEL NOTATION

The notation below and in Table 1 follows Brownie et al. (1993) and Pollock et al. (1990). I expanded the theory of multiple strata mark-recapture models (program MSSURVIV, Brownie et al. 1993) to include information gained by backdating the locations of individuals during time t when capture occurs in time $t + 1$, but not t (Table 1).

Let r denote location, where $r = 1$ denotes that an animal is in stratum 1, and $r = 2$ denotes that an animal is in stratum 2 at time i; the pair rs denotes locations at time i and $i + 1$, respectively. The following statistics are sufficient for the estimation procedure:

R_i^r = banded releases at time i in stratum r.
m_{ij}^{rs} = members of R_i^r that are next caught in stratum s at time j.
s_{ij}^{rs} = members of R_i^r that are captured in time j and are known to have been in stratum s during time $j - 1$ because of *a posteriori* analyses.

For the above, $r = 1, 2. . . , n$; $s = 1, 2,. . . , n$; $i = 1,. . . , t - 1$; $j = 2,. . . , t$.

The following parameters are to be estimated:

ψ_i^{rs} = probability of moving from stratum r to s between sampling occasion i and $i + 1$, given that the animal is alive at i and $i + 1$; $i = 1,. . . , t - 1$.

S_i^r = probability of marked animal on stratum r at time i surviving to $i + 1$; $i = 1,. . . , t - 1$.

p_i^r = probability of animal on stratum r at time i being recaptured at occasion i; $i = 2,. . . , t$.

For the above, $r = 1, 2. . . , n$; $s = 1, 2,. . . , n$.

MODEL STRUCTURE

Given release in the first time period in stratum 1, the probability that an animal will have a capture history of 121 (reflecting that it moved to stratum 2, was captured in stratum 2 in the second time period, moved back to stratum 1, and was captured in stratum 1 in the third time period) is:

$$S_1^1\ (\psi_1^{12})\ (p_2^2)S_2^2(\psi_2^{21})\ p_3^1$$

In contrast, if the same animal is not captured during the second time period, its location during period 2 is unknown. Following Brownie et al. (1993), the probability of an animal having the capture history 101 reflects the sum of two potential paths in a 2-strata system: (1) the animal remained in stratum 1, or (2) it moved to stratum 2 during time period 2:

$$[S_1^1(1 - \psi_1^{12})(1 - p_2^1)S_2^1(1 - \psi_2^{12})p_3^1]$$

$$+ [S_1^1(\psi_1^{12})(1 - p_2^2)S_2^2(\psi_2^{21})p_3^1]$$

However, by using *a posteriori* analyses, such as stable isotopes, after capture of a marked animal in period 3, the capture history 101 may be enhanced to $10^{(r)}1$, where r is the location of the animal during time 2, as determined by stable-isotope or other *a posteriori* analysis. For example, the probability of the capture history $10^{(2)}1$ is:

$$S_1^1(\psi_1^{12})(1 - p_2^2)S_2^2\ (\psi_2^{21})\ p_3^1$$

This model differs from Brownie et al. (1993) in that a stratum assignment can be made in period 2 even when an animal is not captured (indicated by $[1 - p_2^2]$ in the above equation). Following this general pattern, other examples of model structure for various enhanced capture histories can be found in Table 1. Note that this model relies on an initial banded cohort of individuals (R_i^r), and the definitions for m_{ij}^{rs} and s_{ij}^{rs} are conditioned on membership in R_i^r. Thus, the capture history 011 cannot be enhanced (Table 1), even if *a posteriori* information is available for period 1, as the animal was not a member of the released cohort R_1^r.

MODEL ASSUMPTIONS

Assumptions of this model include those of Cormack-Jolly-Seber mark-recapture (Seber 1982, Pollock et al. 1990) and multiple strata mark-recapture (Brownie et al. 1993) models. In addition, this model assumes correct stratum assignment. The resulting estimates of movement between strata will be biased if stratum assignments have errors; this requirement may be more strict than some current stable-isotope analyses provide. For example, Wassenaar and Hobson (2001) stated that their analyses provided good information for discriminating on a north-south basis, but were less efficient at separating prior locations on an east-west basis (see also Hobson et al. 2004). In fact, the goal of most stable-isotope research at present is to discriminate between general locations of a group, by comparing population means and by building regression models to infer connections between geographic strata (e.g., Rubenstein et al. 2002).

Errors in stratum assignments are likely to increase with proximity of geographic strata. However, Chamberlain et al. (1997) used a multiple-isotope analysis to increase the resolution for determining breeding locations of warblers captured on their wintering grounds. Analyses of δD from Bicknell's Thrush (*Catharus bicknelli*) in Quebec have identified locations within a region with a 4° latitude gradient (K. A. Hobson, pers. comm.). In addition, Meehan et al. (2001) estimated a 1.5° latitudinal resolution was possible when estimating the origins of Cooper's Hawks (*Accipiter cooperii*) migrating through the Florida Keys.

Stratum assignment usually is predicated on documented temporal molt patterns (e.g., most migratory birds in North America molt before migration, Hobson 2002) and molecular turnover rates of the animal tissue (Hobson 1999). Therefore, another source of stratum assignment error is the use of tissues that were not grown during the assumed temporal period. Feathers preserve isotope signatures for almost a year,

until molt occurs. So, stratum assignments would normally be limited to the location of the bird during its molt. But, injuries can cause feather loss at any time between molts; such an incident could cause an erroneous stratum assignment.

CAPTURE SIMULATION MODEL

I was not aware of an existing data set that could provide the information needed by this model structure. Therefore, I constructed a simulation model in SAS/IML (SAS Institute 2000) to provide data for this estimation model, and to compare results under various parameter values. Two geographic strata were each initialized with 10 000 simulated birds, which then moved between the two strata during three time intervals (years). Individuals remained in one stratum for one year, and then were allowed to change strata between years. The model was structured to simulate migratory breeding birds that make decisions affecting fidelity to breeding grounds between years (Geramita and Cooke 1982, Wheelwright and Mauck 1998, Flynn et al. 1999, Tiedemann et al. 1999, Suryan and Irons 2001, Doherty et al. 2002).

I used an annual survival rate of 70% for all simulations. Mortality was simulated by choosing a uniformly distributed random number, x_{ij}, between zero and one for each individual j in year i, where i = 1–3 and j equals the number of individuals at the beginning of the interval. If x_{ij} was greater than the annual survival rate (0.70), the individual died during year i. A new x_{ij} was chosen for each live animal.

I derived capture histories for populations under a range of recapture and movement rates. During a given year, the number of birds to be captured in stratum y was determined by multiplying the number of birds alive in stratum y by the preset capture rate for that stratum. Birds were sampled at random without replacement from the set of live animals until the number of birds to be captured was reached; captures were independent between years. Capture rates (p) were common across strata ($p_i^1 = p_i^2$), and were preset to 5%, 10%, and 20% to represent a range of potential capture rates from field studies. Movement rates between the two strata were identical ($\psi_i^{12} = \psi_i^{21}$), and were preset to 20%, 50% and 80%. Three capture and three movement rates combined for a total of nine simulated populations (Fig. 1). Movement was determined in the same fashion as mortality, generating a uniformly distributed random number, x_{ij}, for each live bird. If x_{ij} was less than the preset movement rate, the animal was transferred to the other geographic stratum.

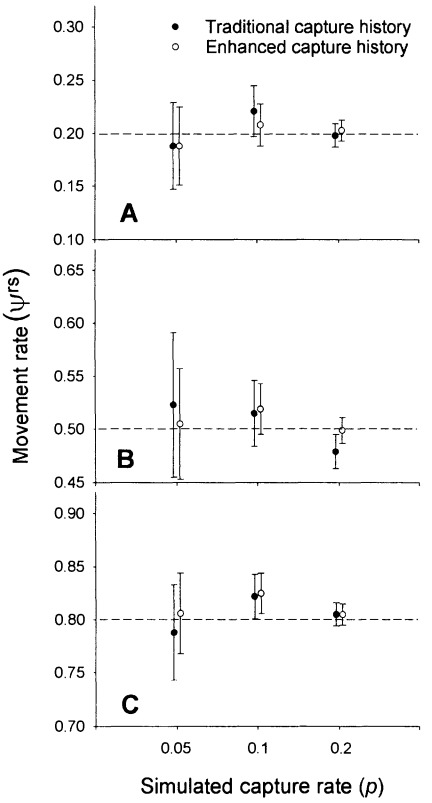

FIGURE 1. Estimates of movement rates using traditional capture histories (filled circles) and capture histories enhanced with *a posteriori* information (unfilled circles) about locations, such as is available from stable-isotope analyses. Rates were estimated from capture simulation models, over three capture rates (x-axis) and three movement rates: (A) $\psi^{rs} = 0.2$, (B) $\psi^{rs} = 0.5$, and (C) $\psi^{rs} = 0.8$. Annual survival in all simulations was set at 0.7. Dashed lines represent the actual movement rate used in the simulation; bars indicate 95% CI.

Capture histories were derived from records of captured birds, with 1 and 2 signifying capture in stratum 1 and stratum 2, respectively. Zero signified a year of no capture. Therefore, if a bird was captured in stratum 2 in year 1 and stratum 1 in year 2, but was not captured anywhere in year 3 (either dead, or alive and not captured), its capture history would be 210.

The computer simulation allowed me to record each individual's location during each year,

despite its capture status. "True knowledge" of each individual's location during noncapture years simulated the *a posteriori* information available from stable-isotope analyses. Therefore, I was able to enhance capture histories by replacing 0s with 1s or 2s, if a noncapture year was followed by a capture of a previously captured individual. Animals in my simulation that benefited from enhancement included those captured in both years 1 and 3 but not in year 2 (capture histories 101, 102, 201, or 202). I assumed that each bird captured in year 3 could have its location in year 2 determined via stable-isotope or other *a posteriori* analyses. Based on this additional information, I updated the capture history to reflect the animal's location. Thus, each animal captured in both year 1 and year 3 had a complete capture history (no zeroes). I used program SURVIV (White 1983) to estimate survival, capture, and movement rates from the simulated capture histories in a multistate model following the methods of Brownie et al. (1993); the enhanced capture histories were analyzed with the model structure in Table 1.

LARGE-SAMPLE APPROXIMATIONS

In addition to the capture simulation model, I performed a large-sample approximation (Nichols et al. 1981) with program SURVIV (White 1983); parameter estimates were derived using the model structure in Table 1. I used this analysis to explore the effect of sample size on the precision of movement estimates.

I used the same model structure, 2-strata system, and SURVIV input file as in the capture simulation models, above. However, I standardized the number of animals in each cohort at either 100, 1000 or 10 000. To perform the approximation, I computed the expected number of animals exhibiting each capture history and used these values as input data for program SURVIV (e.g., if survival, recapture, and movement rates dictated that P(capture history 102|release in stratum 1 and time 1) = 0.05 and the cohort size was 100, then the expected number of animals would be 100 × 0.05 = 5]. For all approximations, I used $S^1 = S^2 = 0.7$, $p^1 = p^2 = 0.2$, and $\psi^{12} = \psi^{21} = 0.5$.

RESULTS

The precision of movement rate estimates improved in all nine permutations of the capture simulation model with the addition of *a posteriori* data (Fig. 1). The coefficient of variation (CV) decreased by an average of 0.013 (11% decrease) when $\psi^{rs} = 0.2$, by 0.017 (24% decrease) when $\psi^{rs} = 0.5$, and by 0.005 (12% decrease) when $\psi^{rs} = 0.8$ ($n = 3$ for all means; Fig. 1).

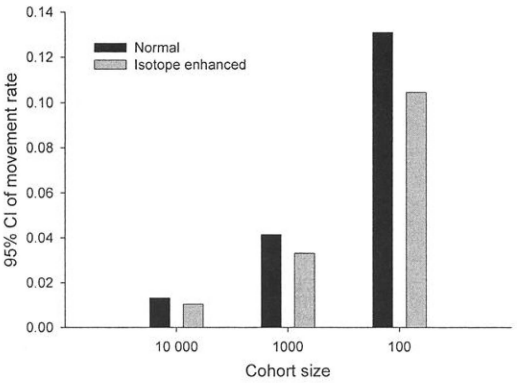

FIGURE 2. Comparison of 95% CI of movement rates for the traditional multistate model structure and an enhanced model structure, for a range of cohort sizes. Estimates were obtained from a large-sample approximation with program SURVIV and incorporated the following parameters: $S^1 = S^2 = 0.70$; $\psi^{12} = \psi^{21} = 0.5$; $p^1 = p^2 = 0.2$.

The enhanced model provided smaller 95% CI for movement rate estimates across all sample sizes, based on large-sample approximations. When the sample size of marked individuals in each subpopulation was 100, the 95% CI width decreased from 0.13 to 0.10 (Fig. 2), reflecting a substantial improvement at a sample size commonly obtained in field research projects.

Survival and recapture rates, and their estimates of precision (SE), remained the same during all simulations. Enhanced capture histories did not bias the estimates of movement rate; of the nine permutations of the capture simulation model, four simulations resulted in slight reductions in the movement rate estimate, three produced slight increases, and two estimates remained the same (Fig. 1).

DISCUSSION

Enhanced capture histories provided more precise estimates of movement in the simulations because more movement information was made available through auxiliary data. In traditional multistate analyses, multiple pathways must be modeled when an animal is captured in years 1 and 3, but not in year 2 (e.g., capture history of

101 or 102 in Table 1). Enhancement of the capture history with auxiliary data reduces the model structure to the pathway actually taken by the animal (Table 1), and therefore increases the precision of the estimate.

As anticipated, survival, capture, and movement rate estimates themselves were unbiased. This method allows the incorporation of additional information regarding movements of animals that would not be available without the use of methods such as stable-isotope analysis. Survival and capture estimates cannot be enhanced, however, because this method requires that a live animal is recaptured to determine the previous year's location.

The model presented could be used to test ecological hypotheses about dispersal and fidelity. As biologists begin to collect physical samples such as feathers with routine avian banding data (Smith et al. 2003), data sets comparable to the simulated data used in my examples will become available. Similar questions are currently being addressed with banding data. For example, Doherty et al. (2002) assessed several fidelity hypotheses with a combined analysis of recaptures and recoveries of Mallards (*Anas platyrhynchos*) banded in the breeding grounds in Alberta and Saskatchewan. Doherty et al. (2002) were able to rigorously estimate fidelity rates, but did not estimate movement rates among breeding strata; they suggested multistate models as a way to test further hypotheses. Similar research, but on a smaller scale, by Robb (2002) and Arnold et al. (2002) explored questions of regional breeding-site fidelity of waterfowl using the same techniques as Doherty et al. (2002). Again, these questions could be addressed at similar scales using recapture data enhanced with stable isotope information.

The described model simply makes use of locations provided in subsequent years. As such, this method is not limited to stable-isotope-enhanced data, nor is it limited to birds. In fact, Hobson (1999) reviewed applications of stable-isotope analyses to many vertebrate and invertebrate species, ranging from barnacles to bats and elephants. As technology advances in other fields (e.g., molecular genetics), it may be possible to apply this model to other data sources, in which information is made available that would determine an animal's location at a previous time.

Movement rates are needed to parameterize spatially based population models (Conroy et al. 1995). My results suggest that the ability to enhance capture histories can improve the precision for estimates of movement. Doherty et al. (2002) suggested that long-held generalizations about the movement rates of animals should be reconsidered after analysis with proper estimation techniques. As stable-isotope research methods are refined, the model presented here has the potential to increase the precision of movement rate estimates in multistate study designs.

ACKNOWLEDGMENTS

I thank J. Nichols, J. Hines, W. Clark, D. Otis, and K. Hobson for discussions leading to the formulation of this model. E. Blankenship, R. Johnson, and S. Hygnstrom provided helpful comments on an early version of this manuscript. R. G. Clark, K. Hobson, J. Nichols, M. Lindberg, and an anonymous reviewer provided valuable reviews. This is Journal Series No. 13845 from the University of Nebraska Agricultural Research Division.

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